RESPIRATION DURING THE REPRODUCTIVE CYCLE IN THE SEA URCHIN, STRONGYLOCENTROTUS PURPURATUS[1]

A. C. GIESE, A. FARMANFARMAIAN,[2] S. HILDEN AND P. DOEZEMA

*Hopkins Marine Station and Department of Biological Sciences,
Stanford University, Stanford, California*

During the reproductive cycle of the purple sea urchin, *Strongylocentrotus purpuratus,* the gonad may grow many-fold within a few months while the other organs show little relative change (Bennett and Giese, 1955; Giese, 1959). The bulk of the sea urchin tissue is found in its body wall, gut and gonad. The gonad of a non-gravid (resting or spent) sea urchin may have less organic matter than its body wall or gut, but the gonad of a gravid animal has about as much organic matter as all of its other tissues combined (Giese, 1966). Increase in the respiratory rate of the sea urchin corresponding to the increase in gonad size may thus be expected if the tissue O_2 demand remains uniform and O_2 supply does not become limiting. A survey of the literature indicates that variations in respiration correlated with the reproductive cycles of echinoderms have not been investigated (Farmanfarmaian, 1966).

To determine the relationship between the rate of respiration and the reproductive state, the respiratory rate was measured on sea urchins of different gonad indices (ratio of gonad to body wet weight × 100) taken at various times during the annual reproductive cycle (Bennett and Giese, 1955). Similar measurements also were made on specific body components (body wall, lantern, perivisceral fluid, gut and gonads) of the animal.

MATERIALS AND METHODS

The sea urchins were collected near Yankee Point (5 miles south of Carmel, California) and at Moss Beach, Pescadero, Pigeon Point, and Pillar Point, California. They were placed in constantly filtered and aerated sea water in the 13° C. constant-temperature room (at Stanford) or in running sea water at ambient sea water temperature (at Pacific Grove). The animals were not fed in captivity. For studies on whole animals it was necessary to pick out individuals that could be placed inside the respirometric flasks (4 cm. diameter); animals of similar size were also used for studies on body components. The urchins used were about 3.5 cm. in test diameters and varied between 13 and 26 gm. in wet weight. They were placed individually in large respirometric flasks and covered with about 15 ml. sea water. In general, standard Warburg-Barcroft respirometry was employed (see Farmanfarmaian, 1959). Occasionally a sea urchin in a respirometric flask lifts a portion of its surface above sea water. Consequently the Q_{O_2} values for entire sea urchins may on such occasions be somewhat higher than expected because respira-

[2] Now at Pahlavi University, Shiraz, Iran.

tion is higher in air than in water (Farmanfarmaian, 1959). Urchins were watched when possible during experiments and note taken of movement out of water; such data were not used.

Body components were obtained from urchins 3 to 6 cm. in test diameter and 15–26 gm. in wet weight. To remove all debris resulting from excision of body components, each piece was washed 3 to 6 times in filtered sea water. Each piece of body component (about 0.2 to 1.0 g. wet weight, depending upon the tissue) was weighed (Mettler balance), and placed in the Warburg flask in 2 to 4 ml. filtered sea water.

The perivisceral fluid bathing the tissues of an echinoderm is essentially similar to sea water in constitution (Robertson, 1953). In a number of trials the respiration of equal aliquots of body components was found to be the same in perivisceral fluid and in sea water. Consequently, for simplicity, in all subsequent experiments the body components were placed in filtered sea water for respirometry.

With the precautions noted above no bacterial growth was observable over 2 to 5 hours of experimentation with either whole animals or body components. In all experiments reported the respiratory rate (a rising straight line plotting total respiration against time) remained constant for the duration of measurement. This further confirms that oxygen uptake due to bacterial growth was not significant. Because cutting may liberate nutrients from body components, antibiotics (15 γ streptomycin and 4 γ penicillin per ml.; see Skinner, 1962) were tested in sea water. No difference in respiration was observed between samples of the same body components with and without antibiotics. Therefore, their use was discontinued.

All manometric calibrations were performed by injecting a known volume of air from a calibrated syringe. Since the amount of tissue or size of the urchin differed in each experiment, calibrations were made at the beginning or conclusion of each experiment.

To obtain the rate of respiration per unit nitrogen, entire sea urchins were digested with sulfuric acid and the nitrogen content of an aliquot of the digested urchin was determined by the micro-Kjeldahl using the Markham distillation method (Markham, 1942). In practice, each sea urchin was drained on a towel and weighed. It was then opened and the perivisceral fluid drained, measured and dried. Next, the gonads were removed and their wet weight determined. The body wall, Aristotle's lantern, and the gut (washed free of contents) were also drained, weighed wet, and dried. Finally, all these tissues were combined, ground and aliquots were digested. The total nitrogen has been taken as a measure of the tissue content of an animal (Zeuthen, 1947).

All the sea urchins used in the latter part of the present study on whole animals were starved for several days to several weeks before use. Starvation was necessary because urchins fed to satiation defecate continually, sometimes even after two days of starvation. The bacteria in the fecal material would make respiratory determinations meaningless. Urchins from which body components were to be removed for respirometry were also comparably starved. The respiratory rates of the urchins (and tissues) are lower than those previously reported (Farmanfarmaian and Giese, 1963), possibly because starvation decreases the respiratory rate in *S. purpuratus* (Farmanfarmaian, 1966). Desirable as control of nutrition

might have seemed, it was not possible to feed the urchins at Stanford because of the large volumes of sea water required for daily cleaning. Another factor which may determine the Q_{O_2} level is temperature acclimation, which occurs in a few days (Farmanfarmaian and Giese, 1963). The urchins are kept in a constant temperature (13° C.) at Stanford. They are subjected to higher and varying temperatures at the Marine Station. The data for animals studied at each of the laboratories are, however, relatively consistent.

RESULTS

1. *Rate of respiration of whole sea urchins of different gonad indices*

The total nitrogen in a sea urchin of a given size doubles during the growth of the gonad from the immature state to the fully gravid condition, indicating that the tissue in the sea urchin has doubled. Yet, as seen from Figure 1A, there is essentially no change in the respiratory rate per unit wet weight when the gonad index increases from 3 to 20. For a sea urchin of a given size and weight this rate is about constant regardless of its gonad index. The increase in size of the gonad does not entail a proportional increase in total wet weight of the sea urchin, because as the gonad grows, the amount of perivisceral fluid remaining inside the test decreases.[3] Since the specific gravity of the gonad is only slightly greater than that of the perivisceral fluid, increase in the quantity of gonad at the expense of perivisceral fluid has little effect on the total wet weight of the urchin.[4]

If the rate of respiration for unit wet weight does not increase with increase in the bulk of the gonads and the corresponding increase in organic content of the specimens, then the average rate of respiration per unit of organic matter in the animal must decline as the animal becomes more gravid. This is borne out when the respiratory rate is expressed in terms of nitrogen content in Figure 1B; as the gonad index increases, Q_{O_2} per unit nitrogen declines. This means that either the tissue in the gonad (or other tissues) becomes metabolically relatively less active, or the oxygen supply becomes limiting as the gonads grow. The respiration of the sea urchin body components was therefore investigated in order to determine which of these factors is involved in the reduction of Q_{O_2} during gonad growth.

2. *The respiratory rate of sea urchin body components*

The rate of respiration was determined for each of the sea urchin body components to ascertain the contribution of each component to the respiration of individuals 15 to 26 grams wet weight.

From data for the average respiration of sea urchin body components in Table I, it is evident that the Q_{O_2} for the perivisceral fluid is negligible. The Q_{O_2} for the lantern is low; the Q_{O_2} for ovary and body wall, intermediate; and the Q_{O_2} for testis and gut, very high. The rate of respiration of a body component appears to be similar from animal to animal, the data being fairly consistent as indicated by the standard deviations, except for the gut and testes. Part of the variability in

---

[3] The perivisceral fluid values for sea urchins of gonad indices 1.0–3.2, 3.3–5.5, 5.6–7.0, 7.1–11.2 and 11.3–14.9 are 30.4 ±1.0, 25.5 ±2.4, 25.8 ± 4.3, 23.2 ± 3.5 and 21.6 ± 3.3, respectively.

[4] The other variable determining the amount of perivisceral fluid in an urchin is the amount of food stored in the intestinal festoons of the animal.

mature testis Q_{O_2} may result from the liberation of sperm, activating them to different degrees, although the respiratory rate of testes with active sperm was not always high. It therefore seemed best to consider the data for testes in two categories: those with a high rate of respiration (A in Table I) and those with a low rate of respiration (B in Table I).

From the product of the Q_{O_2} for each of the body components and the component index $\dfrac{\text{(component wet weight} \times 100)}{\text{body wet weight}}$ it is possible to arrive at the theoretical oxygen consumption for each component constituting the sea urchin body. For a sea urchin 15–26 grams wet weight the body wall constitutes about 57.8% of the mass, the lantern 4.8%, the perivisceral fluid 26.8% (18.7% to 34.2%), the gut 4.6% and the gonads (depending upon the phase in the reproductive cycle) from 1.4% to 19.0% in the female and from 1.2% to 21.7% in the male. The product of each component index and the Q_{O_2} for the component is given in Table
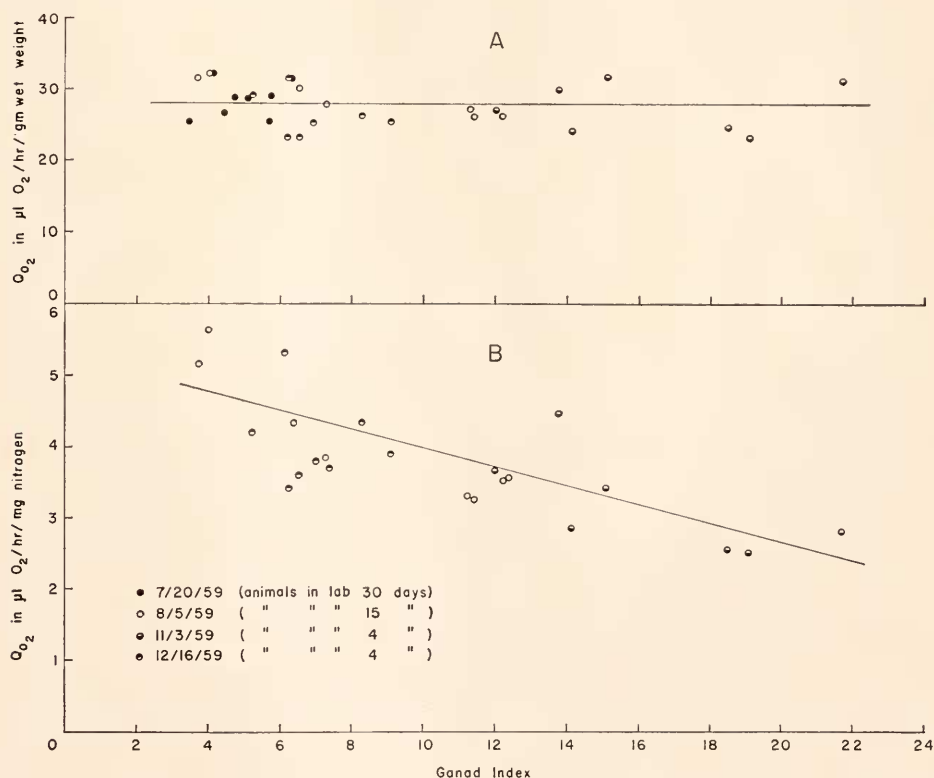

FIGURE 1A. Oxygen consumption of sea urchins in μl. O_2/hour/gram wet weight in relation to gonad index. A second group of data on 46 small sea urchins gathered during the 1964–65 season gave essentially the same results as the data cited here. These data covered a gonad index range of 0.5 to 15 for males and 1.5 to 8.5 for females.

FIGURE 1B. Oxygen consumption of sea urchins in μl. O_2/hour/mg. nitrogen in relation to gonad index. Experiments in A and B were done at the Hopkins Marine Station.

II (Column A × B). The ratio of each product to the sum of the products of the body components times $100 \left(\dfrac{A \times B \times 100}{\Sigma A \times B} \right)$ gives the fraction of the theoretical respiration attributable to a given component (column 7). Both values for testis (see Table I) were used in these calculations for reasons cited above.

From the data in Table II it is evident that in the non-gravid sea urchin the body wall probably accounts for most of the respiration (72.7% in a female of gonad index 1.0 to 71.9% in a male of gonad index 1.0). In these sea urchins the gonad could account for only a small fraction of the respiration (1.6% of the respiration in the female and about 2.7% of the respiration of the male). When the gonad index reaches 20 at the height of the breeding season the fraction of respiration attributable to the gonads increases. The increase in gonad tissue is then expected to increase the respiration of the whole animal by 30% in the case of females, and 51% in the case of males (Table II, last column; if the high value for testis respiration is used (Table IA), the increase for the male is much greater:

TABLE I

Oxygen consumption (Q_{O_2} in μl. O_2/hour/gram wet weight) of body components in sea urchins 15–20 grams wet weight

Body component (B.C.)	B.C. index*	Q_{O_2}**	Number of experiments
Body wall	57.8 ± 7.5	28.3 ± 6.5	38
Lantern	4.8 ± 0.7	13.8 ± 4.7	17
Perivisceral fluid	26.8(18.7–34.2)	1.1 ± 0.8	9
Gut	4.6 ± .8	102.8 ± 33.3	35
Ovary	4.4(1.4–8.2)	36.6 ± 4.4	10
Testis A		145.0 ± 13.9	5
B	6.0(1.2–11.3)	62.1 ± 16.2	19

* The values following the ± sign are standard deviations
** For testis A values are for experiments with very high Q_{O_2}, B values for considerably lower Q_{O_2} (see text).

124%). This expectation is reinforced by the finding that there was no consistent decrease in the oxygen demand of any tissue measured *in vitro* as the urchin became gravid. Thus the body wall and gut from males of gonad index 3–5.9 and 18–20.9 had Q_{O_2} values of 24.4 and 26.6, and 73.1 and 70.7, respectively. Testes and ovaries from urchins of gonad index 3–5.9 and 12–14.9 had Q_{O_2} values of 59.4 and 54.0, and 27.6 and 35.9, respectively.[5] Therefore, the expected increase in the oxygen uptake of the whole animal as it becomes gravid is not compensated for by reduction in the oxygen demand of any tissue and yet Figure 1A shows that the expected increase in fact does not occur.

Direct comparisons were made of total oxygen consumption of an intact sea urchin measured in a large respirometric vessel and subsequently, the total oxygen consumption as determined by summation of the oxygen consumption of its dissected body components. In sea urchins of low gonad index the difference between

[5] Sea urchins larger than 20 grams had to be included in these samples to get a sufficient span of gonad index.

the oxygen consumption measured in these two ways is usually not great but becomes striking, particularly for males of high gonad index. A total of 21 sea urchins were studied in this manner. The average respiration determined by summation of respiration of body components was greater than the respiration measured on the whole animal, verifying the assumptions in Table II. The theoretical

TABLE II

Oxygen consumption (Q_{O_2} in μl. O_2/hour/gram wet weight) of body components and the theoretical respiration of the entire 20-gram sea urchin calculated from these data*

Sex and state of urchin	Body component	A Component index	B Q_{O_2}	(A×B)	Σ(A×B)	% of total respiration $\frac{A \times B}{\Sigma(A \times B)} \times 100$	Theoretical respiration (A×B) for 20-gram urchin	$\frac{Q_{O_2} \text{ gravid} \times 100}{Q_{O_2} \text{ non-gravid}}$
♀ low G I**	Body wall	57.8	28.3	1635.7		72.7		
	Lantern	4.8	13.8	66.2		2.9		
	Fluid***	31.8	1.1	35.0		1.6		
	Gut	4.6	102.8	472.9		21.0		
	Gonad	1.0	36.6	36.6	2246.4	1.6	449.3	
♀ high G I	Body wall	57.8	28.3	1635.7		55.9		
	Lantern	4.8	13.8	66.2		2.3		
	Fluid	12.8	1.1	14.1		0.5		
	Gut	4.6	102.8	472.9		16.1		
	Gonad	20.0	36.6	732.0	2920.9	25.0	584.2	130
♂ low G I	Body wall	57.8	28.3	1635.7		71.9		
	Lantern	4.8	13.8	66.2		2.9		
	Fluid	31.8	1.1	35.0		1.6		
	Gut	4.6	102.8	472.9		20.8		
	Gonad	1.0	62.1	62.0	2271.8	2.7	454.4	
♂ high G I low testis Q_{O_2}	Body wall	57.8	28.3	1635.7		47.7		
	Lantern	4.8	13.8	66.2		1.9		
	Fluid	12.8	1.1	14.1		0.4		
	Gut	4.6	102.8	472.9		13.8		
	Gonad	20.0	62.1	1240.0	3428.9	36.2	685.8	151
♂ high G I high testis Q_{O_2}	Body wall	57.8	28.3	1635.7		32.1		
	Lantern	4.8	13.8	66.2		1.3		
	Fluid	12.8	1.1	14.1		0.3		
	Gut	4.6	102.8	472.9		9.3		
	Gonad	20.0	145.0	2900.0	5088.9	57.0	1017.7	224

* The Q_{O_2} data for body components are taken from Table 1.
** G I refers to gonad index.
*** Perivisceral fluid.

respiration determined by summation of the respiration of body components of gravid urchins was usually greater than that calculated in Table II, especially in males. Thus the theoretical respiration for a male of gonad index 7.0 was 103% greater than that directly determined on the whole urchin, and for a male of gonad index 11.2 it was 179% greater. However, the data in Table II were caculated from average values for many measurements on each of the body components.

There exists a possibility that the total oxygen consumption of a whole gravid sea urchin is less than that of its components measured separately because of factors other than lack of oxygen. Thus, tissue cells need not respire at the same rate inside the sea urchin as when they are removed, a case in point being sperm activated to swimming resulting in oxygen consumption higher than inside the testis of the urchin, although the respiratory rate was not high in all cases in which actively swimming sperm were seen. Possibly endocrine or other regulatory agents, lacking in dissected components, may determine the rate of respiration of the tissues inside an urchin although no evidence exists for such factors. However, the total respiration of the rat, which has a well-developed endocrine system, is only slightly more than the sum of the respiration of its parts (Field *et al.,* 1939). The total respiration of an intact snail which also has endocrines may be equal to the sum of the respiration of its parts, although usually it is less (Kerkut and Laverack, 1957). It seems more likely, however, that availability of oxygen to tissues is probably the major factor limiting respiration of tissues in the intact sea urchin. Oxygen tension of perivisceral fluids in several species of echinoderms tested was much lower than prevails in the bathing sea water; no such tests have yet been made on the purple sea urchin (see review in Farmanfarmaian, 1966).

Discussion

The data reported in this paper demonstrate that there is no increase in respiration (Q_{O_2}) of the purple sea urchin corresponding to the increase in tissue during growth of the gonad from resting to gravid state. The data suggest that the expected augmentation in the total oxygen uptake of the gravid animal fails to occur because of insufficiency of the oxygen supply. The limits of oxygen supply are set by the ambient oxygen tension, the respiratory surface, and oxygen transport to the internal organs. Since the oxygen tension of the water containing the sea urchins was uniform in all the experiments, this parameter may be set aside from the present discussion. The respiratory surface and oxygen transport to the internal organs, however, are important matters for consideration. The test surface and the external appendages take up their oxygen from the ambient waters directly, and therefore there is no oxygen attenuation. The internal organs, on the other hand, receive their oxygen supply mainly through the ambulacral podia and ampullae. Within the coelom dissolved oxygen is transported by ciliary currents and other convection transport (Farmanfarmaian, 1959).

The haemal system, which may play a role in distribution of nutrients (Boolootian and Campbell, 1964), is unlikely to participate in distribution of oxygen because there is no way for oxygen to enter it except through the perivisceral fluid, and no respiratory pigment is present. Thus, the internal supply of oxygen is limited by the respiratory surface and the internal transport. When the sea urchin becomes gravid and the gonad tissue increases by 10- to 20-fold (and the nitrogen content of the sea urchin doubles), there is no commensurate increase either in the respiratory surface or in the internal oxygen transport. This presumably results in oxygen attenuation in the perivisceral fluid and relative oxygen unsaturation of tissues which are far from the respiratory surface (see review in Farmanfarmaian, 1966). However, no measurements of the oxygen tension of the perivisceral fluid of the purple sea urchin have yet been made. Oxygen un-

saturation has, however, been demonstrated indirectly in echinoderms, including the purple sea urchin, as well as in other animals which, within limits, "conform" to the oxygen tension of their atmosphere. Asteroids such as *Patiria miniata, Asterias rubens,* and *Asterias forbesi* increase or reduce oxygen consumption in proportion to the ambient tension within a definite range (Hyman, 1929; Koller and Meyer, 1933; Meyer, 1935; Maloeuf, 1937). Such is said to be true for the purple sea urchin as well (Hyman, 1929, p. 532). Nomura (1926) reported that in the range of 0.72–5.7 cc. O_2/l., the rate of oxygen consumption in the sea cucumber *Paracaudina chilensis* is directly proportional to the oxygen tension of the medium. When these or other "conforming" organisms are minced, the oxygen consumption of the minced tissue is independent of the oxygen tension and is constant (Harnisch, 1932; Meyer, 1935). In short, the limitations of the respiratory surface and internal transport are eliminated by the mincing process; there is then no oxygen attenuation or oxygen unsaturation of the internal organs. Increase in ambient oxygen tension, therefore, does not then change the rate of oxygen consumption.

The respiratory rate of echinoderms increases with increase in environmental temperature, reaching a maximum between 26 and 30° C. in various animals (Farmanfarmaian and Giese, 1963; Farmanfarmaian, 1966). In the case of *S. purpuratus,* the respiratory rate at 20° C. is double that at 10° C. (not allowing time for acclimation). Under these conditions, while the metabolic rate increases, the respiratory surface and the ambient oxygen tension do not change (although the amount of oxygen dissolved in the sea water decreases). The increase in oxygen consumption observed at the higher temperature may be attributed to increased direct oxygen uptake by the external tissues (chiefly the body wall, which in the size range studied, makes up more than $\frac{1}{2}$ of the urchin bulk) and increase in ciliary convection transport of oxygen to the internal organs, allowing increased respiration of at least the surfaces of the organs if not of the deeper cells.

Finally, the discrepancy between Figures 1A and 1B becomes clear on the basis of the following considerations: Within a given reproductive cycle there is no significant change in the total wet weight of the animal because changes in amount of perivisceral fluid generally compensate for changes in gonad weight. Total respiration appears to be limited by the oxygen supply which is nearly constant throughout the reproductive season. The respiratory rate expressed in terms of wet weight, therefore, does not change significantly within a reproductive cycle (Fig. 1A). On the other hand, gram for gram, the total nitrogen of the gonad is much higher than that of the perivisceral fluid. There is a real and substantial increase in the total nitrogen of the animal, due to the growth of the gonads within a reproductive season. The respiratory rate expressed in terms of total nitrogen decreases as the gonads grow, although total respiration remains nearly constant throughout a reproductive cycle (Fig. 1B).

SUMMARY

1. The oxygen consumption of small sea urchins differing in gonad index, studied by Warburg-Barcroft manometry, is 26 to 31 μl. O_2 per hour per g. wet weight, or between 3.0 to 5.6 μl. O_2 per hour per mg. nitrogen.

2. The rate of oxygen consumption per unit wet weight is approximately the same regardless of gonad index of the animals.

3. The gonad index measures the size of gonad relative to the entire body weight. In a sea urchin the wet weight does not change appreciably within a reproductive cycle as the gonad index increases because the perivisceral fluid, of much the same specific gravity as the tissues, is displaced by the gonads.

4. With increase in gonad index, however, the bulk of organic material as measured by nitrogen content in a sea urchin increases, ultimately doubling. Consequently, when the rate of respiration is measured per unit nitrogen content, it is found to fall with rise in gonad index.

5. When gonads and other body components are removed from the body, and oxygen consumption measured in sea water in equilibrium with air, their rate of respiration is approximately the same regardless of size or gonad index of the animal from which they came. When the gonad increases in size, the expected total respiration of the sea urchin, as determined by summing the respiration of its body components, is therefore greater than the respiration measured on the intact animal in water in equilibrium with air.

6. The rate of respiration of sea urchins is probably limited by the respiratory surface and convection transport of oxygen to the internal organs. Increase in the bulk of internal tissue due to gonad growth does not result in increased total respiration by the animal. Presumably, instead, coelomic oxygen tension becomes attenuated, resulting in the relative oxygen unsaturation of the internal tissues.

LITERATURE CITED

BENNETT, J., AND A. C. GIESE, 1955. The annual reproductive and nutritional cycles in two western sea urchins. *Biol. Bull.,* **109**: 226–237.

BOOLOOTIAN, R. A., AND J. L. CAMPBELL, 1964. A primitive heart in the echinoid *Strongylocentrotus purpuratus. Science,* **145**: 173–175.

FARMANFARMAIAN, A., 1959. The respiratory surface of the sea urchin, *Strongylocentrotus purpuratus.* Ph.D. Thesis, Stanford University.

FARMANFARMAIAN, A., 1966. The respiratory physiology of echinoderms. *In:* Physiology of Echinodermata, R. A. Boolootian, Ed. Wiley, New York (in press).

FARMANFARMAIAN, A., AND A. C. GIESE, 1963. Thermal tolerance and acclimation in the purple sea urchin *Strongylocentrotus purpuratus. Physiol. Zoöl.,* **36**: 237–243.

FIELD, J., III, H. S. BELDING AND A. W. MARTIN, 1939. An analysis of the relation between basal metabolism and summated tissue respiration in the rat. I. The post-pubertal rat. *J. Cell. Comp. Physiol.,* **14**: 143–157.

GIESE, A. C., 1959. Annual reproductive cycles of marine invertebrates. *Ann. Rev. Physiol.,* **21**: 547–576.

GIESE, A. C., 1966. On the biochemical constitution of some echinoderms. *In:* Physiology of Echinodermata, R. A. Boolootian, Ed. Wiley, New York (in press).

HARNISCH, O., 1932. Studien zur Physiologie des Gaswechsels von Tieren ohne Regulierung der Sauerstoffaufnahme bei wechselnden O_2 Partialdruck. *Zeitschr. vergl. Physiol.,* **16**: 335–344.

HYMAN, L. H., 1929. The effect of oxygen tension on oxygen consumption in some echinoderms. *Physiol. Zoöl.,* **2**: 505–534.

KERKUT, G. A., AND M. S. LAVERACK, 1957. The respiration of *Helix pomatia*—a balance sheet. *J. Exp. Biol.,* **34**: 97–105.

KOLLER, G., AND H. MEYER, 1933. Versuche über Atmung der Echinodermen (*Asterias rubens* und *Echinus milliaris*). *Biol. Zbl.,* **53**: 655–661.

MALOEUF, N., 1937. Studies on the respiration and osmoregulation of animals. *Zeitschr. vergl. Physiol.,* **25**: 1–28.

MARKHAM, R., 1942. A steam distillation apparatus suitable for micro-Kjeldahl analysis. *Biochem. J.*, **36**: 790–791.

MEYER, H., 1935. Die Atmung von *Asterias rubens* und ihre Abhängigkeit von verschiedenen Aussenfactoren. *Zool. Jb. (Abt. Zool.)*, **55**: 349–398.

NOMURA, S., 1926. The influence of oxygen tension on the rate of oxygen consumption in *Caudina*. *Sci. Rep. Tohoku Univ., Ser. 4, Biol.*, **2**: 133–138.

ROBERTSON, J. D., 1953. Further studies on ionic regulation in marine invertebrates. *J. Exp. Biol.*, **30**: 277–296.

SKINNER, D. M., 1962. The structure and metabolism of a crustacean integumentary tissue during a molt cycle. *Biol. Bull.*, **123**: 635–647.

ZEUTHEN, E., 1947. Oxygen uptake as related to body size in organisms. *Quart. Rev. Biol.*, **28**: 1–12.